

THE ECOLOGICAL NICHES OF *LEPTOSPERMUM SCOPARIUM* AND *L. ERICOIDES* (ANGIOSPERMAE: MYRTACEAE)

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ABSTRACT

Field observations and some limited experimental work permit approximate circumscription of the niches of *Leptospermum scoparium* and *L. ericoides* with respect to each other and to forest tree species.

INTRODUCTION

Attempts to distinguish differences between the niches of organisms living in natural communities are often difficult. This applies particularly to plants. Like simple metazoans, their distributions are mainly directly controlled by factors of the physical environment and their social interactions are uncomplicated (Miller 1967). Nevertheless their ecological relationships are subtle and hard to define. Tree species, for example, may live with root and shoot systems in close proximity for long periods, ostensibly using the same limited pool of resources, especially of nutrients and water. It is not easy to demonstrate that there are differences in the requirements for these resources or the abilities of the species to utilize them. Natural plant communities are mixtures of species with similar and overlapping tolerances but it is assumed that the species are sufficiently different to permit them to behave only as partial competitors (Whittaker 1965). Competition by vigorous, dominant species may, of course, exclude other species from a plant community. Some of the differences which enable plant species to coexist when resources are limited are expressed in their morphology, but others, resulting from physiological differences, are cryptic. Plants have evolved in communities and it may be assumed that natural selection has caused divergences which minimize competition. The possession of such differences is analogous to the phenomenon of character displacement in animals (Hutchinson 1953, Lack 1947). Thus the spatial sympatry of plants in communities is in fact permitted by a degree of ecological differentiation.

It is doubtful if the boundaries of the fundamental niche of any plant species have been so thoroughly explored that all the environmental parameters defining it are known, although they are reasonably well known for some cultivated species. Many ecologists have (sometimes unwittingly) contributed to the knowledge of the ecological niche of the species they were studying by measuring some of the niche parameters. Further observations and experiments are needed to test the universal validity of the ecological niche concept in plant communities.

Field observations of the distribution and relative behaviour patterns of various organisms have led to a wider understanding than could be obtained in the microcosm experiments which have generated much of the theory of ecological niches. In particular this applies to studies of the partitioning of the available environment by organisms in response to particular regimes of environmental factors. Such, for example, are the studies of Connell (1961) on species of barnacle on rocky shores, Terborgh (1971) on birds on a mountain side in Peru, Whittaker (1967) on the quantities and distributions of tree species on hill country in the U.S. and Beals (1969) on the distributions of shrubs on hillsides in Ethiopia. Most of these papers are descriptions of the behaviour of species parallel to environmental gradients. Gradients provide suitable natural field experiments for studies of this kind, but other kinds of distribution are also useful.

The behaviour of two *Leptospermum* species in unmanaged communities allows partial definition of their niches. New Zealand is a natural laboratory for this kind of study because of the existence of many relatively diverse ecological situations.

THE *LEPTOSPERMUM* SPECIES

Leptospermum is a genus of the Myrtaceae with about 35 species in Australia, New Caledonia, Malaya and New Zealand (three). The two common New Zealand members of the genus, *L. scoparium* (manuka) and *L. ericoides* (kanuka), are moderately short-lived shrubby species. Both are important in the vegetation and, although they are not particularly closely related phylogenetically, they have overlapping ecological behaviour. *L. scoparium* will be treated in some detail before a comparison is made with *L. ericoides*. Although the ecological amplitude of *L. scoparium* is fairly well known in a general sense, its relationship to any particular environmental parameter is not. For example, the complexities of its tolerance of temperature extremes or requirements for nutrients cannot be precisely specified. Nevertheless the niche width can be gauged from the wide range of undisturbed and disturbed habitats in which it is found. I would like to examine, first, the limitation placed upon *L. scoparium* by competition from forest trees.

HABITATS OF *LEPTOSPERMUM SCOPARIUM* IN ANCIENT TIMES

The nature of the vegetation in the New Zealand environment, some 1500 years ago, may be reasonably well reconstructed from evidences such as those presented by Molloy et al. (1963), Molloy (1969) and from knowledge of the present-day patterns of vegetation in undisturbed localities. At this time, before the Maori came to New Zealand, forest occurred throughout most of the country, from sea-level to about 1500 m. *Leptospermum* species were relatively restricted in their distribution. The main stands of *L. scoparium* were:

- (1) On the Volcanic Plateau of the central North Island which had been deforested by a catastrophic volcanic eruption about

1800 years B.P. (Healy, Vucetich and Pullar 1964). Earlier eruptions there and elsewhere would have had similar but possibly less widespread effects on the forests, either by starting fires or by overwhelming them with ash. *L. scoparium* was quick to colonize such areas and formed an early phase in autogenic succession back to forest.

(2) In various other places, e.g. North Auckland, which were potentially forested, but temporarily disturbed by natural fires, *L. scoparium* played a similar successional role.

(3) On young sites on landslides which were quickly colonized by *Leptospermum* before they reverted to forest, e.g., in Fiordland (Mark et al. 1964).

Otherwise, sites occupied by *L. scoparium* were:

(4) On the Canterbury Plains and Central Otago on soils too dry for forest (Molloy 1969, Burrell 1965). *L. ericoides* was usually more important than *L. scoparium* in these areas.

(5) On flood plains of some of the large rivers, occupying sites where periodic renewal of soils by deposition or disturbance by flooding were such that dense forest could not develop, e.g., in the Hurunui and Waiau valleys. *L. ericoides* was more important in such areas.

(6) On lake margins where periodic flooding limited tree growth, e.g., around lakes Manapouri and Te Anau.

(7) On bog or swamp margins, e.g., in many places in Westland and western Southland. More extensive continuous stands were present on some of the relatively fertile peat lands and also on extremely poor, waterlogged mineral soils in western Fiordland and Westland.

(8) On coasts, in a variety of habitats such as sand dunes, e.g., in south Westland and Farewell Spit; shingle beach ridges, cliffs and windswept headlands, e.g., near Wellington, in various parts of Westland and Fiordland.

(9) In a few areas at timberline, e.g., in western Fiordland.

(10) Forming extensive stands on cool, cloudy, windswept parts of Stewart Island and islands to the south-west (Cockayne 1909, Dr B.A. Fineran, pers. comm.).

(11) Forming an understorey in stunted, open forest on poor, gleyed soils, e.g., in parts of Fiordland.

These apparently diverse habitats have one thing in common. They are extreme in some way and marginal for the growth of tall woody plants. In several instances they are sandwiched between forest on the one side and an extreme habitat (a lake, a bog, an alpine environment) on the other. In the seven site categories (4) - (10), *L. scoparium* vegetation must be regarded as the dominant, mature, self-sustaining plant cover, maintained because the stringent environment prevents taller competitors from ousting it. Such mature communities of *Leptospermum* have canopies open enough to allow light penetration to the ground so that regeneration can occur.

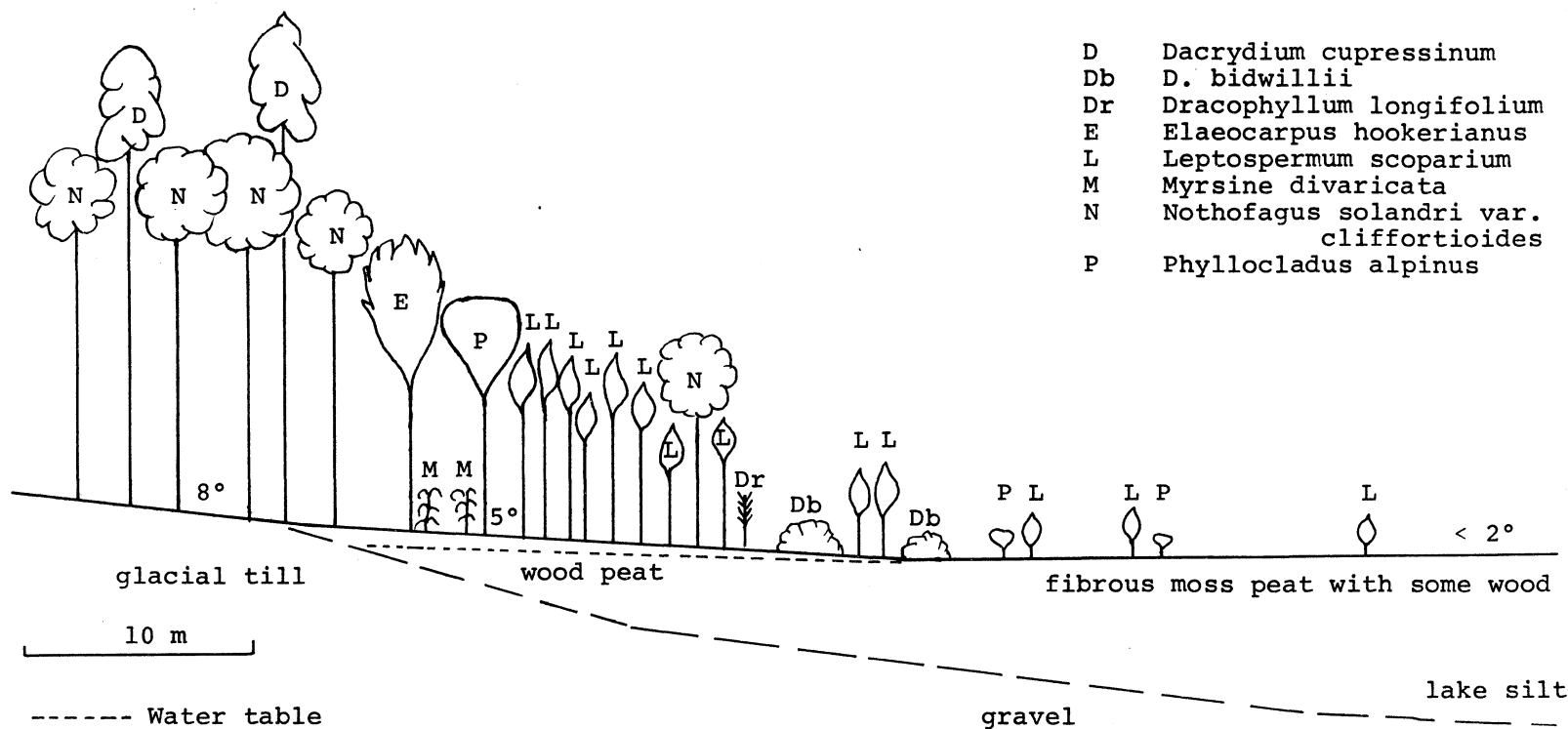


Fig. 1. Diagram of vegetation at the margin of Richters Rock mire, Manapouri. Similar patterns occur round other forest-surrounded mires. To scale except for shrubs below 2 m in height.

DISTURBED HABITATS

When the Maori and later the Europeans arrived in New Zealand, they began to destroy the predominant forest cover most extensively by fire. Subsequently there was a great expansion of *Leptospermum* vegetation. Both species occupied a wide range of conditions, but *L. scoparium* was able to inhabit wetter, more infertile soils and sites at higher altitudes and in cooler localities than *L. ericoides*. Clearly both species are opportunists with great potential for spread onto open sites. Both produce vast quantities of seed. In such conditions they form dense stands, but, usually, insufficient light penetrates the dense canopy to permit the growth of *Leptospermum* seedlings and saplings. The stands do not regenerate unless the site is rendered too extreme for forest redevelopment. *Leptospermum* species usually are supplanted by taller species whose seedlings and saplings are shade tolerant. Eventually the *Leptospermum* canopy is overtopped and the *Leptospermum* plants die for lack of light. On extreme sites, the canopy opens up as the stand ages, permitting the growth of juvenile *Leptospermum* plants.

One situation which I know well exemplifies the process of change after forest disturbance. Bogs near Lakes Manapouri and Te Anau have a marginal band of *L. scoparium* between taller, dense forest and the open mire surface (Fig. 1). *L. scoparium* occurs on the mire surface, if at all, only in the form of stunted, scattered bushes. It can be inferred that the continually wet, very acid, nutrient-poor conditions prevailing there are marginal even for this tolerant species. If the site is burnt and the surrounding forest destroyed, the stunted *L. scoparium* plants on the bog surface are replaced only very slowly, or not at all. But, released from competition, the species becomes dominant on adjacent dry land. Stands of *L. scoparium*, originating in this way, covered tens of thousands of hectares in the Te Anau basin until they were recently cleared for farmland. Forest soils and charcoal testify that, previous to Maori occupation, the whole area was densely forested except for the open bogs, lake margins and similar sites.

If the *Leptospermum* stands were left alone much of the area would, presumably, eventually return to forest. On some surfaces with strongly leached soils, however, the fires brought about the loss, by further rapid leaching, of nutrients previously held in the ecosystem by tight nutrient cycles. With the nutrients gone, poor, gleyed soils remain and it is likely that *L. scoparium* now forms an equilibrium vegetation on these soils, as it does on similar soils in Westland and North Auckland. Very slow nutrient enrichment might eventually allow forest to re-develop after several centuries.

FUNDAMENTAL NICHE OF *LEPTOSPERMUM SCOPARIUM*

Consideration of the ecological behaviour of *L. scoparium* in all its complexities reveals the relative limitations placed on the species by external environmental parameters and by competition. The fundamental niche of *L. scoparium* is broader than those of virtually all forest-dominants in New Zealand, for

TABLE 1. COMPARISON OF ECOLOGICAL CHARACTERISTICS OF TWO LEPTOSPERMUM SPECIES

	<u>L. scoparium</u>	<u>L. ericoides</u>
Age at which first flowering and seeding occurs	3-6 yr	ca 6 yr
Germination of seed	Current year's seed can germinate but is usually not shed till one or more years later. Release by environmental shock (fire, drought, cold).	Current year's seed all shed April - June.
Seed viability	Up to six weeks after shedding.	Up to six weeks after shedding.
Seed dispersal	Wind (whole capsules water, animals).	Wind.
Height	(0.5) - 6.0 - (10 m)	6.0 - 10 - (20 m)
Longevity	30 - 40 - (200 yr)	80 - 150 - (250 yr)
Growth rate	Rapid.	Faster than <u>L. scoparium</u> in the most suitable conditions.
Resistance of capsules to fire	Relatively resistant.	Less resistant.
Rainfall regime within which present	500 - 5000 mm per annum.	500 - 2500 mm per annum.
Tolerance of waterlogging of soils	Tolerated.	Not tolerated.
Altitudinal limits		
(a) Dry climates (ca 500 mm rainfall p.a.)	1000 m (below timberline).	860 m
(b) Mesic climates (ca 1500 mm p.a.)	900 m (below timberline).	500 m
(c) Supermesic climates (ca 5000 mm p.a.)	900 m (at timberline).	300 m
Reaction to manuka blight attacks	Usually killed except above 600 m and in supermesic areas.	Usually survives.

in their absence it can inhabit all the sites which the trees can occupy. *L. scoparium* can also extend a little further into various kinds of extreme habitat, e.g., it is tolerant of lower soil fertility, higher soil moisture, lower soil moisture and greater exposure to wind and salt spray than the tree species. The realized niche of *L. scoparium* is very much narrower in places where undisturbed forest occurs. Although it is a generalist species in many respects, *L. scoparium* is specialized in having a rapid and effective means of spread onto bared soils, in having shade-intolerant replacement phases in its life history and in having limited potential for height growth. The forest trees are more generalized in the characteristics which allow them to supersede it. As in many other groups, the general adaptability of *L. scoparium* is not correlated with competitive superiority.

COMPARISON OF THE NICHES OF *LEPTOSPERMUM SCOPARIUM* AND *L. ERICOIDES*

A comparison of two ecologically similar species should enable their relative fundamental niche widths and their mutual competitive effects to be seen. *L. ericoides* occurs, together with *L. scoparium* or alone, in disturbed and undisturbed sites in many parts of New Zealand. The fundamental niche of *L. ericoides* seems to be narrower than that of *L. scoparium* in several respects because it is unable to inhabit some of the habitats available to them both. Various differences between the two species are summarized in Table 1. One would expect that in many habitats *L. scoparium* would have a competitive advantage and the field evidence shows that this is so. For example, relatively little *L. ericoides* occurs in Westland where *L. scoparium* occupies large areas. Wet soils favour the latter and *L. ericoides* is most usually found on well-drained alluvial soils. Similarly *L. scoparium* dominates on infertile soils and, because of its seeding habit and resistant capsules is better able than *L. ericoides* to survive persistent fires.

Nevertheless *L. ericoides* gains the advantage over *L. scoparium* in a number of circumstances. Burrell (1965) showed how the resistance of the former to manuka blight (*Eriococcus orariensis*) allows it to supplant *L. scoparium*. *L. ericoides* forms a reservoir of infection which eventually causes the elimination of the susceptible *L. scoparium*. On dry sites with relatively fertile soils, *L. ericoides* is also able to withstand greater competition from tree species than *L. scoparium* apparently because its seedlings are more tolerant of shade and root competition (Burrell 1965). On Kapiti I., following fire and farming, an initial growth of *L. scoparium* was replaced by *L. ericoides* after about 100 years because the latter is potentially taller, faster growing and longer-lived. *L. ericoides*, in turn, is supplanted by forest trees (Esler 1967).

Thus the relative behaviour of the two species in competition depends on their ability to interact with the local environmental conditions. There is insufficient evidence to allow more precise definition of their realized niches with respect to each other. This must await growth experiments in controlled environments. The realized niche of *L. ericoides* with respect to trees of the forest proper is similar to that of *L. scoparium*.

rium, with the exception that, apparently, it is a better competitor in shaded conditions. Its potentially taller growth habit also benefits it under these circumstances.

It is likely that there are diverse, genotypically-different races of the *Leptospermum* species, adapted to local conditions. The total niche width for the species will be greater than for local populations.

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